

Changes in tree species diversity and dominance across a disturbance gradient in Nepalese Sal (*Shorea robusta* Gaertn. f.) forests

Indra Prasad Sapkota • Mulualet Tigabu • Per Christer Odén

Received: 2009-01-28; Accepted: 2009-06-22
© Northeast Forestry University and Springer-Verlag Berlin Heidelberg 2010

Abstract: Disturbance is often touted as a management tool, as moderate disturbance is believed to enhance diversity; thus an understanding of frequent and fluctuating disturbance regimes in forests and their effects on stand structure, dominance and diversity is very crucial. Here, the effects of different disturbance regimes, along a gradient, on diversity and dominance of five *Shorea robusta* Gaertn. f.-dominated forests were investigated in 25 one-ha plots in Nepal. A total of 67 tree species were recorded; of which 41 species were encountered in least disturbed and 10 species in heavily disturbed forest. Significant variations among forests were observed for all measures of alpha diversity. Alpha diversity measures declined linearly along a disturbance gradient while dominance increased linearly. Relative basal area of *S. robusta* increased as the level of disturbance increased, which in turn produced more than two-fold higher important value index in heavily disturbed forest than the least disturbed forest. All alpha diversity measures declined in an order of three with increasing relative basal area of *S. robusta*. The similarity in species composition between each pair of disturbed forests was generally low (Jaccard's similarity index < 57%), suggesting a higher Beta diversity. It can be concluded that diversity of Sal forests declines with increasing magnitude of disturbance, which in turn favors a higher dominance of *S. robusta*. Controlling the population of the dominant species, mainly *S. robusta*, is recommended to enhance diversity and to achieve multiple-use forest management objectives.

Keywords: Human pressure; disturbance ecology; species richness; alpha diversity; important value index

Foundation project: The study was supported by Swedish International Development Cooperation Agency (SIDA).

The online version is available at <http://www.springerlink.com>

Indra Prasad Sapkota (✉) • Mulualet Tigabu • Per Christer Odén
Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, Tropical Silviculture and Seed Science Group, P.O. Box 101, SE-230 53 Alnarp, Sweden. Tel: +46 40 41 53 94; Fax: +46 40 41 53 98; E-mail: sapkotai@yahoo.com

Responsible editor: Chai Ruihai

Introduction

Biological diversity is essential for human survival and economic well being (Sagar et al. 2003; Zhu et al. 2007). However, unprecedented rate of deforestation and degradation of tropical forests accelerated the loss of biological diversity along with the water sources and non-timber forest products (Lamb et al. 2005). The loss of biological diversity is perhaps the most crucial concern for human survival as it influences all ecological services and livelihoods. The United Nations Conference on Environment and Development in Rio de Janeiro in 1992 identified human exploitation as a key reason for the loss of biodiversity, and put forward this human-vegetation nexus as the main subject for discussion especially since the Rio declaration (Tárrega et al. 2006).

In general, natural as well as human disturbances often lead to altered environmental conditions, which influence the process that can both augment and erode species diversity in a forest community (Kennard et al. 2002; Sagar et al. 2003). These disturbances determine forest dynamics and tree diversity at both local and regional scale (Hubbell et al. 1999; Sheil 1999; Ramirez-Marcial et al. 2001; Kennard et al. 2002). Changes in structural attributes of forests have often been attributed to disturbance regimes (Kennard et al. 2002) involving mostly a single factor that is limited in extent, e.g. selective logging (Cannon et al. 1994; Nagaike et al. 1999; Ramirez-Marcial et al. 2001; Sapkota et al. 2009a, b). It has also been argued that species richness and diversity are invariably affected by frequent and fluctuating disturbances of low-intensity e.g. grazing and browsing, firewood and fodder extraction suggesting the importance of combined effect of multiple factors (Sagar et al. 2003; Zhu et al. 2007).

Despite general agreements on the role of disturbances of a suitable intensity in maintaining species diversity (Connell 1978; Vetaas 1997; Sheil 1999; Hubbell 2001; Sheil and Burslem 2003), the detailed processes that structure the diversity following disturbance remain unclear yet (van Gemerden et al. 2003).

Hubbell et al. (1999) and Sheil and Burslem (2003) tested intermediate disturbance hypothesis (Connell 1978) in Barro Colorado Island and came up with contrasting conclusions. Sheil and Burslem (2003) believed that the intermediate disturbance hypothesis is still relevant in explaining higher species richness as too much disturbance leads to the loss of late-successional species and too little disturbance leads to exclusion of species adapted to colonizing younger sites. On the other hand, Hubbell et al. (1999) opined that a recruitment limitation, i.e. the failure of a species to recruit in all sites normally outweigh disturbances. They urged that although disturbances in mature forest do enlarge the choices of available niches, these would not necessarily be filled by most adapted species, but rather by those whose propagules are abundant enough at right place and right time.

Amidst these arguments, many researchers showed that not all disturbance agents can increase species diversity (Fulbright 2004; Tárrega et al. 2006). Lindenmayer and Franklin (2002) opined that human disturbance regimes are different from the natural ones, e.g., for the forest ecosystem, the human disturbance does not maintain the same connectivity, landscape heterogeneity and stand structural complexity, as what natural disturbance does. Therefore, the impacts of human disturbances on species diversity are generally different, depending on the type and intensity of disturbances. For example, few studies in Indian *S. robusta* forests (hereafter referred as Sal forests) showed that lower magnitude of anthropogenic disturbances often lead to higher tree species diversity (Pande 1999; Sagar et al. 2003). Pandey and Shukla (2001) further emphasized that degraded Sal forests profoundly regenerate clonally, which maintain minimal species diversity. But, these studies lack clarity on combined effect of 'time since', 'type of' and 'level of' disturbances in maintaining higher species diversity. Therefore, multiple factors of disturbances need further discussion in order to understand disturbance-diversity nexus.

Common anthropogenic disturbances like burnings, grazing, browsing, timber harvesting, fodder and fuel-wood extraction in Sal forests have widely been reported from most parts of India (Pande 1999; Pandey and Shukla 2001; Sagar et al. 2003) and Nepal (Webb and Sah 2003; Timilsina et al. 2007; Sapkota et al. 2009a,b). In addition, these forests supply a major part of subsistence needs like fuel-wood, livestock feed, animal bedding and compost and other minor forest products for more than 80% of rural population in Nepalese low land (Webb and Sah 2003). Given the immense pressures from decade-long frequent and fluctuating anthropogenic disturbances and the high conservation values as wildlife corridors (Timilsina et al. 2007), the Sal forests of Nepal needs immediate conservation/management attentions. Therefore, an understanding of combined effects of frequent and fluctuating disturbances on dominance, stand structure and diversity of Sal forests is very crucial to ensure the twin management goals- supporting livelihood of poor people and biodiversity conservation. Thus, the present study was undertaken to examine the changes in tree species diversity and dominance along a disturbance gradient in Sal forests by combining effects of multiple disturbance factors. The hypotheses of the study were: (1) Tree species diversity declines while increasing dominance along a

disturbance gradient from low to high magnitude; (2) Higher relative basal area of the dominant tree species negatively affects the tree species diversity.

Materials and methods

Study area

This study was conducted in five seasonally-dry deciduous Sal forests (Jackson 1994) in the Nawalparasi district of Nepal (Fig. 1). These forests, which represent climatic climax vegetation in each locality (Anonymous, 1994; Webb and Sah, 2003), are located between 27°28'–27°94'N and 83°56'–84°21' E at similar altitudes, and they are managed by the local people as community and buffer zone forests and by the State (Table 1). The study forests are growing on an alluvial plain with similar geological characteristics to the Gangetic plain of India in the south, while the underlying sediments originate from tertiary Siwalik material in the north (Anonymous 1994). The Siwalik hills are composed of coarsely bedded stones, crystalline rocks, clays and conglomerates. The texture of the soil (from 0–10 cm depth) varies from sandy to loam with varying chemical property (Table 2). The climate in the area is tropical to sub-tropical and a typical year can be divided into three main seasons: cold, hot and rainy. May and June have the highest mean maximum temperature (34.6°C), while the coldest months are December and January (9.9°C). Maximum rainfall occurs during the monsoon season (June–September) with an average monthly rainfall of 531.3 mm (Fig. 2). Dew falls from December to February.

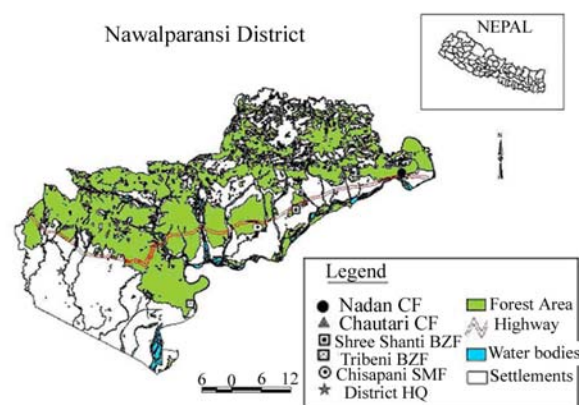


Fig. 1 Location of seasonally dry deciduous *Shorea robusta* dominated forests represented in this study.

Prior to 1963, the forests in the study area were intact and nearly pristine with high faunal and floral diversity. Later, malarial eradication program, construction of the East-West national highway and political unrest reduced the forest cover considerably. The continuous flow of migrating people from the hills to these areas has caused further forest degradation and encroachment. According to the forest management plan for this region

(Anonymous 1994), the annual deforestation rate between 1964 and 1990 was 2%–2.4% of the national forests. In this 25-year period, approximately half of the forest area in the district was either degraded or converted to other uses. Recently, the management and ownership rights of some forests have been transferred from the State to the local communities. Although protec-

tion rules have been imposed following this transfer of ownership, no specific management tools have been applied in these forests. All forests are managed with the same approach of protection with selective logging of dead and diseased trees. Moreover, no major changes in forest use patterns have been observed following the ownership change.

Table 1. Geographical location and management regimes of study forests.

Forests	Latitude	Longitude	Elevation range (m)	Management regime*	Azimuth for the transect line
Sushta Triveni	27° 28.342'	83° 56.495'	105–175	Buffer zone forest (BZF)	320°
Chautari	27° 42.948'	84° 14.481'	305–360	Community forest (CF)	360°
Nandan	27° 42.606'	84° 21.544'	195–295	Community forest (CF)	40°
Danda Chisapani	27° 42.948'	84° 03.534'	160–186	State managed forest (SMF)	300°
Shree Shanti	27° 38.490'	84° 08.667'	170–200	Buffer zone forest (BZF)	20°

*The management responsibilities and ownership are recently assigned to the local community in CF and BZF. Government owns and manages the entire forests in SMF. Buffer zone is a forest area between settlements and the core protected forests.

Table 2. Physico-chemical properties of soils in the study forests (Mean \pm SE).

Forests	pH	Organic Matter (%)	N (%)	P (kg/ha)	K (kg/ha)	Sand (%)	Silt (%)	Clay (%)	Moisture (%)	Type
Sushta Triveni	6.3 \pm 0.30	0.79 \pm 0.19	0.06 \pm 0.01	12.2 \pm 0.4	173.0 \pm 49.3	52.4 \pm 3.1	36.2 \pm 3.8	11.4 \pm 1.01	6.3 \pm 0.9	Sandy
Chautari	5.2 \pm 0.07	2.1 \pm 0.15	0.13 \pm 0.01	3.0 \pm 0.5	413.2 \pm 40.8	41.9 \pm 1.3	35.7 \pm 1.1	22.4 \pm 1.07	12.3 \pm 1.3	Sandy-clay loam
Nandan	5.2 \pm 0.10	1.2 \pm 0.13	0.28 \pm 0.2	4.1 \pm 1.1	236.0 \pm 73.6	47.3 \pm 3.9	33.6 \pm 1.8	19.1 \pm 3.4	7.1 \pm 1.1	Sandy-clay loam
Danda Chisapani	5.5 \pm 0.10	2.0 \pm 0.2	0.13 \pm 0.01	26.1 \pm 9.7	471.2 \pm 54.4	40.2 \pm 5.5	34.2 \pm 2.9	25.6 \pm 3.5	11.0 \pm 1.0	Loam
Shree Shanti	5.2 \pm 0.09	1.5 \pm 0.21	0.26 \pm 0.15	18.6 \pm 5.7	346.1 \pm 20.0	43.4 \pm 2.3	38.0 \pm 1.9	18.6 \pm 1.9	11.7 \pm 1.2	Loam

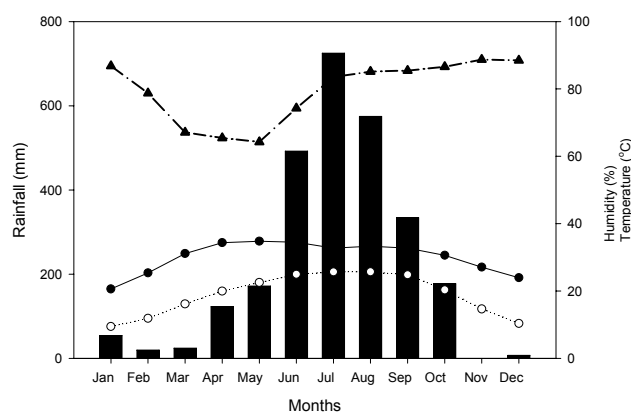


Fig. 2 Mean annual rainfall (vertical bars), relative humidity (triangles), and mean maximum (points) and minimum (circles) temperatures of the study area during the period 2003–2005.

Sampling and inventory

The forests were selected based on a reconnaissance survey and discussion on their current management regimes with forest officers. Detailed inventories for each forest were carried out from October 2006 to March 2007 using the quadrat method. In each forest, a constant azimuth (Table 1) was chosen for lying the transect lines from the settlement to the core zone of the forest. In each forest, five 1-ha plots were established along the right-

hand side of each transect successively at 200 m intervals from the settlements. Each 1-ha plot was then divided into 25 sub-plots (each 20 m \times 20 m) for sampling individuals with > 20 cm diameter at breast height (dbh). A square quadrat of 25 m² was also laid out at the left corner of each sub-plot for sampling individuals with 1.5–20 cm dbh. The dbh of each individual was measured using a digital caliper and a diameter-tape (when possible). Species were identified in situ when possible, and by comparison with voucher specimens from the National Herbarium.

Assessment of disturbance

Prior to the inventory, all possible disturbance regimes were discussed with local forest users, and the major disturbance regimes that were occurring in a frequent and fluctuating manner and having multiple and simultaneous effects on the vegetation were identified. These included damages by windthrow, harvesting, cutting, lopping, breakage, browsing, uprooting, crown openness, herbivory and site disturbance (e.g. footpaths, cart trails). No fire disturbance has previously been observed in these forests, thus not considered in this study. During the forest inventory, all individuals showing signs of damage were identified and counted, and their collar diameters were measured in the same sub-plots and quadrats. 'Time since' disturbance was estimated and categorized as 'recent' (< 2 years), 'old' (> 2 years to < 10 years) or 'very old' (> 10 years). These categories were based on visual inspection of the bark, stem and leaf residues around the

stumps, stump freshness, stump color, termite mounds and cracks in the remaining stumps. Crown openness was estimated using a densiometer. Disturbance due to herbivores was estimated by counting the number of wallowed and/or disturbed spots (e.g. by rhinos, wild pigs, deer, rodents, hedgehogs etc.) and animal feces (as indicators of their presence). Footpaths and trails, as indicators of site disturbance, were measured using a linear tape.

Based on the relative impact of major disturbance indicators in each forest, a Disturbance Impact Factor (DIF) was derived for placing the forests along a disturbance gradient (see Sagar et al. 2003 for details). In each forest, DIF values for browsing, cutting, lopping, breaking and uprooting were obtained from estimates of the relative density and basal area of damaged individuals (seedlings, saplings, poles and trees) as follows:

- (1) Relative density of damaged individuals = sum of density of damaged individuals / total density (damaged + normal)
- (2) Relative basal area of damaged individuals = sum of basal area of damaged individuals / total basal area (damaged + normal)
- (3) The forest with the lowest value of relative density of damaged individuals was assigned an impact factor of 1 for each disturbance indicator.
- (4) The forest with the lowest value of relative basal area of

damaged individuals was assigned an impact factor of 1 for each disturbance indicator.

(5) For other forests, the relative impact factor was calculated as follows:

(a) Relative density of damaged individuals in forest of interest / relative density of damaged individuals in the forest with lowest value;

(b) Relative basal area of damaged individuals in the forest of interest / relative basal area of damaged individuals in the forest with lowest value.

The impact factor was also calculated according to 'time since disturbance' for each disturbance indicator separately. For other disturbances (crown openness, herbivory and footpath/trails etc.), the forest with the lowest number of cases or measurement values was assigned an impact factor of 1 for each disturbance indicator. For other forests, the relative impact factor was calculated as follows: the number of cases or measurement values in the forest of interest / the number of cases or measurement values in the forests with the lowest number of cases or measurement values.

Finally, the relative impact factor for each disturbance indicator was summed up, and the forests were placed along a disturbance gradient from I to V (Table 3).

Table 3. Relative impact factor for each disturbance indicator and an estimated disturbance impact factor (DIF) for each forest.

Forests	Browsing etc (seedling density)	Lopping etc (sapling/pole density)*	Lopping etc (sapling/pole stump basal area)*	Harvesting etc (adult tree den- sity)*	Harvesting etc (adult tree stump basal area)*	Crown openness	Wild-lives and herbi- vores	Foot path and trails	Animal feces	Total	Disturbance category /gradient
Sushta Triveni	1	2.6	2.5	3	3	1	14.1	1	1	29.2	I
Chautari	4	6.4	4.5	7.1	6	1.2	15.7	31.6	3.7	80.2	II
Nandan	6	13.8	18.4	7	8.2	1.3	3.5	30.1	2.3	90.6	III
Danda Chisapani	5.9	8.8	9.9	16	25.8	1.4	1	34.3	1.3	104.4	IV
Shree Shanti	5.5	23	9.4	8.7	10.9	1.2	32.8	64.4	5.1	161	V

*Impact factor for these disturbances was first computed for recent, old and very old groups separately and then summed up.

Data analysis

The total number of species, number of unique species and number of species with single individual per forest were computed. To compare species richness and composition of the plots, we computed number of species (S), species per individual ratio (S_c / N) and Important Value Index (IVI) of the species. IVI of the species was calculated by summing up the relative frequency, relative basal area and relative density. Alpha diversity in relation to disturbance was examined using the following diversity measures per plot that were subjected to One-Way ANOVA:

1. Margalef's index of species richness (SR),

$$SR = S_c - 1 / \ln(N) \quad (1)$$

2. Shannon-Wiener index (H'),

$$H' = -\sum p_i \log_2 p_i \quad (2)$$

where, p_i is the proportion of individuals belonging to species i , N is total number of individuals, and S_c is total number of species. Means that exhibited significant differences were compared using Tukey's test with 5 % probability level. In addition, Jaccard's index of similarity (IS) was calculated for assessing Beta diversity as follows:

$$IS = \{c / (a + b + c)\} \times 100 \quad (3)$$

where, c is number of species common to both forest stands, a is the number of species unique to forest stand 1, and b is the number of species unique to forest stand 2.

To examine dominance, we computed Simpson's index for each forest and tested for significant difference using One-way ANOVA. The Simpson's index was calculated using the equation:

$$D = \sum (n_i(n_i - 1) / (N(N - 1))) \quad (4)$$

where, N and n_i are the total number of individuals and the total number of individuals of the i th species, respectively. The dominance-diversity curve was drawn by plotting IVI against species rank from highest to lowest IVI (Whittaker 1970).

To further examine the pattern of change in species composition, diversity and dominance across the disturbance gradient, a linear regression was fitted using species richness, species-individual ratio, Margalef's, Shannon-Weiner's and Simpson's indexes as dependent variable (y) and DIF as independent (x). As *S. robusta* was found to be the most dominant species in all forests, we examined the relationship between the relative basal area of *S. robusta* (y) and DIF (x) using linear regression. To examine whether the change in alpha diversity across the disturbance gradient is related to the dominance of *S. robusta*, the relationship between each diversity measures (y) and relative basal area (%) of *S. robusta* (x) were explored by curve fitting. All statistical analyses were performed using SPSS version 15 (SPSS for Windows, Chicago: SPSS Inc.).

Results

Tree species diversity

A total of 67 species representing 60 genera and 37 families were recorded in five seasonally dry Sal forests; of which the least disturbed forest had the highest species richness, while heavily disturbed forest had the lowest (Table 4). Similarly, higher number of unique species was observed in least and moderately disturbed forests (I and II) than heavily disturbed one (V). Some species were represented by single individual, which were large in the least and moderately disturbed forests (I and II) compared to heavily disturbed forest (V). The species represented by a single individual varied from 27 to 50% of the total number of species along a disturbance gradient. With regard to the alpha diversity measures, significant variation was observed for mean species richness, Margalef's index of species richness, Shannon-Wiener's index and species per individual across the disturbance gradient (Table 4). All diversity measures were higher in the least disturbed forest than in the heavily disturbed one. Beta diversity, as evidenced from lower species similarity, was higher between the forests subjected to least (I) and heavily disturbed forest (V), while it was lower between forests subjected to moderate disturbance (II and III) that had high species similarity (Table 5). Nevertheless, the Beta diversity was generally high between the other disturbed forests.

Table 4. Summary of the species composition, diversity and dominance measures for five seasonally dry *S. robusta* forests along a disturbance gradient (mean \pm SE). Means followed by the same letter across rows are not significantly different.

Disturbance gradient	Diversity measures							
	Total number of species	No. of unique species	No. of species with single individual	Mean species richness	Margalef's index	Shannon-Wiener index	Species per individual	Simpson's index
I	41	16	12	22 \pm 2a	9.31 \pm 0.89a	3.23 \pm 0.26a	0.13 \pm 0.02a	0.18 \pm 0.03a
II	37	11	14	16 \pm 1b	6.39 \pm 0.63b	1.75 \pm 0.41b	0.08 \pm 0.02ab	0.54 \pm 0.11ab
III	28	2	8	15 \pm 1b	5.69 \pm 0.42b	1.96 \pm 0.273b	0.06 \pm 0.009bc	0.44 \pm 0.09ab
IV	22	2	6	11 \pm 1b	4.31 \pm 0.50b	1.20 \pm 0.24bc	0.05 \pm 0.002bc	0.66 \pm 0.07bc
V	10	4	5	4 \pm 1c	1.29 \pm 0.43c	0.29 \pm 0.10c	0.07 \pm 0.009c	0.92 \pm 0.03c
F				27.11	23.73	15.14	9.68	12.9
p				<0.001	<0.001	<0.001	<0.001	<0.001

Table 5. Similarity in species composition between disturbed forests represented in the present study, based on Jaccard's coefficient.

	Disturbance gradient				
	I	II	III	IV	V
I	100	41.7	31.9	35.7	13.6
II		100	56.3	42.2	18.8
III			100	38.1	18.5
IV				100	15.0
V					100

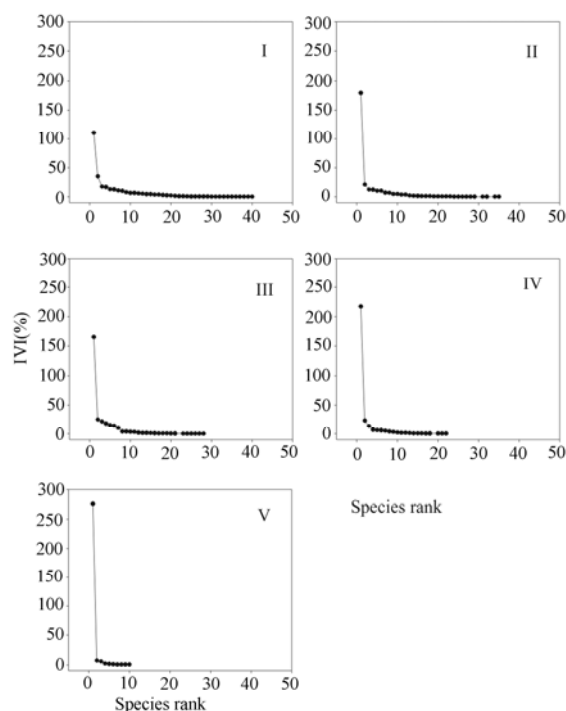
Tree species dominance

Simpson's dominance index varied significantly among forests;

the highest being for the heavily disturbed forests and the lowest for the least disturbed one (Table 4). The dominance-diversity curves in all forests displayed a log series distribution (Fig. 3), where the majority of the species had lower IVI while few species had higher values. Irrespective of the magnitude of disturbance, *S. robusta* appeared to be the most dominant species with the highest IVI (Table 6). The IVI of *S. robusta* differed highly among forests; being the highest in heavily disturbed (V) compared to the least disturbed one (I). *Lagerstroemia parviflora*, *Mallotus philippensis*, *Wendlandia coriacea* and *Symplocos* spp. were co-dominant species across the disturbance gradient from I to IV, respectively (Table 6).

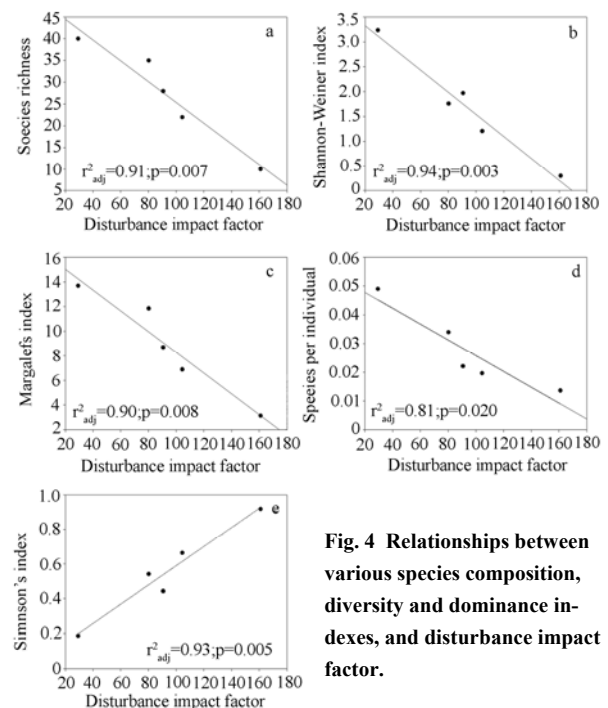
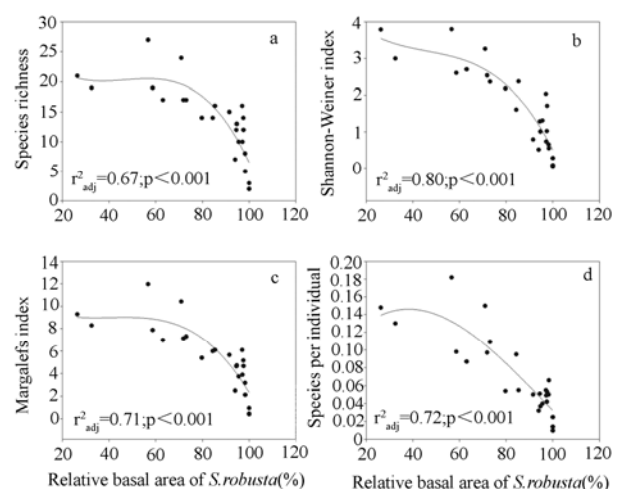
Table 6. Important value indices of 25 tree species and their families across a disturbance gradient.

Family	Species	Disturbance gradient				
		I	II	III	IV	V
Dipterocarpaceae	<i>Shorea robusta</i>	111	179	165	217	274
Lythraceae	<i>Lagerstroemia parviflora</i>	35	13	11	5	8
Combretaceae	<i>Terminalia alata</i>	18	13	22	14	-
Euphorbiaceae	<i>Mallotus philippensis</i>	17	21	-	-	3
Anacardiaceae	<i>Semecarpus anacardium</i>	13	7	19	7	1
Combretaceae	<i>Anogeissus latifolius</i>	13	-	-	-	-
Leguminosae	<i>Desmodium oojeinense</i>	11	-	-	-	-
Sapindaceae	<i>Schleichera oleosa</i>	10	-	-	-	-
Cyperaceae	<i>Mariscus sumatrensis</i>	8	-	-	-	-
Symplocaceae	<i>Symplocos</i> spp.	7	5	4	23	7
Anacardiaceae	<i>Spondias cytheria</i>	-	11	-	-	-
Rubiaceae	<i>Anthocephalus cadamba</i>	-	11	-	-	-
Myrtaceae	<i>Syzygium cumini</i>	-	7	14	-	-
Leguminosae	<i>Cassia fistula</i>	-	5	-	4	-
Rubiaceae	<i>Wendlandia coriacea</i>	-	-	25	-	-
Anacardiaceae	<i>Semecarpus</i> spp.	-	-	15	-	-
Rubiaceae	<i>Adina cardifolia</i>	-	-	4	-	-
Sterculiaceae	<i>Pterospermum lanceae-folium</i>	-	-	4	-	-
Cornaceae	<i>Cornus oblonga</i>	-	-	-	7	-
Euphorbiaceae	<i>Sapium insigne</i>	-	-	-	6	1
Myrtaceae	<i>Eugenia operculata</i>	-	-	-	4	-
Lecythidaceae	<i>Careya arborea</i>	-	-	-	3	-
Euphorbiaceae	<i>Aporosa octandra</i>	-	-	-	-	2
Moraceae	<i>Ficus religiosa</i>	-	-	-	-	2
Euphorbiaceae	<i>Trewia nudiflora</i>	-	-	-	-	1
Unidentified		-	-	-	-	1

**Fig. 3 Dominance-diversity curve based on IVI of tree species and species rank for each forest along the disturbance gradient.**

Relationships among disturbance, tree species dominance and diversity

The regression analyses revealed that more than 80% of the decline in alpha diversity measures across the disturbance gradient was explained by the DIF (Fig. 4). DIF explained 93% of the increase in Simpson's dominance index across the disturbance gradient. The relative basal area of *S. robusta* increased linearly as the level of DIF increased ($r^2_{adj} = 0.77$; $p = 0.032$). All alpha diversity measures declined by the order of three with increasing relative basal area of *S. robusta* (Fig. 5).

**Fig. 4 Relationships between various species composition, diversity and dominance indexes, and disturbance impact factor.****Fig. 5 Relationships between various species composition and diversity measures, and relative basal area of *Shorea robusta* (%).**

Discussion

In the present study, we found different combinations of species across the disturbance gradient. Decrease in total number of species along the disturbance gradient and small number of unique species on more disturbed forests may reflect high exploitation pressure (Sagar et al. 2003). The disappearance of some sensitive woody species at its recruitment stage was often observed due to grazing pressure (Onaindia et al. 2004). The presence of large number of species with only one individual in the least disturbed forests (I and II) compared to other forests might be due to recruitment limitations. These species could be of pioneer species that respond only to major disturbances, not to small gaps (Brown and Whitmore 1992). Our finding is consistent with Sagar et al. (2003), who observed 18 to 30% of Indian dry forest species (> 30 cm circumference at breast height) were represented by a single individual.

The alpha diversity measures followed an inverse trend with disturbance gradient, which indicated that least disturbances facilitate species diversity. It is preliminarily so because least disturbed forests often experience low level of species exploitation and also ensure higher resource availability (Sagar et al. 2003). Collins et al. (1995) also found a significant monotonic decline in species diversity with increasing frequency of experimental disturbances. The decline in alpha diversity across disturbance gradient is also related to an increase in the dominance of a particular species along the same gradient, as evidenced from the negative relationship between relative basal area of the most dominant species, *S. robusta*, and alpha diversity measures in our study.

Extremely higher Beta diversity between the least disturbed forest (I) and heavily disturbed one (V) and the lower Beta diversity between the moderately disturbed forests (II and III) may be attributed to the magnitude of differences in species-individual ratio found there. The former pair showed higher difference, while the latter showed lower. Sagar et al. (2003) also found a positive relationship between Beta diversity and species-individual ratio. Decreasing trend of species-individual ratio along a disturbance gradient in the present study may suggest that disturbances were crucial factor altering the pattern of 'between habitat diversity' in Sal forest community. It also indicates that the study forests lack the homogeneous level of species exploitation. Such phenomenon may lead a species-rich forest to a species-poor (Sagar and Singh 2006).

Simpson's dominance index was substantially higher in heavily disturbed than in the least disturbed forest. Too much disturbance leads to the loss of late-successional species while favoring early successional and/or disturbance-tolerant species. In the present study, *S. robusta* was found to be the dominant species in all disturbed forests, but highly dominant in heavily disturbed forest. Its relative basal area increased linearly across the disturbance gradient. This phenomenon could be related to its ability to regenerate aggressively by suckers following disturbances (Pandey and Shukla 2001; Gautam and Devoe 2006; Sapkota et

al. 2009a, b). It is also argued that due to strong light demanding character of *S. robusta* (Jackson 1994; Gautam and Devoe 2006), disturbance-led light availability favors its seedling recruitment process (Webb and Sah, 2003; Sapkota et al. 2009a, b). In addition, repeated exploitation of some species such as *Terminalia alata*, *Adina cardifolia*, *Terminalia bellirica*, *Syzigium cumini*, *Eugenia operculata* and *Careya arborea* for fodder and fuelwood in these forests (pers. obs.) could be of another factor that may alter the course of succession (Swamy et al. 2000), leading to single species dominance in the system. Our finding on single species dominance is consistent with the study made in Doon valley (Pande 1999) and in southern forests of India (Swamy et al. 2000). The occurrence of different co-dominant species along a disturbance gradient can be attributed to their ability to tolerate competition for space and resources from *S. robusta* and the choice and extent of exploitation of the co-dominants by the local people. For example, *Wendlandia coriacea* and *Symplocos* spp. are co-dominant species in relatively disturbed forests due to the fact that they are least preferred species by the local people.

Conclusions

The present study illustrated that tree diversity declines while dominance increases linearly along a disturbance gradient. Disturbance appears to favor single species dominance of *S. robusta*. The change in tree diversity is also related to relative basal area of the dominant tree species. In view of fostering tree species diversity in seasonally dry deciduous Sal forests, the young population of *S. robusta* needs to be reduced in order to maximize the chances of light, space, water and minerals to other species. Due attention should be given to the level of forest exploitation and choice of species for extraction in order to maintain species richness. We suggest enrichment planting of under populated species like *Terminalia alata*, *Terminalia bellirica*, *Careya arborea*, *Syzigium cumini* and *Eugenia operculata*. We also suggest an amendment to the forest Act by including under populated and unique species, as identified here, into the list of protected species.

Acknowledgements

We thank Bijaya Raj Paudel, Padam Prasad Nepal, Bhairab Prasad Ghimire and Lok Raj Nepal for their help with logistics. We are grateful to Shesh Kanta Bhandari, Bishnu Bahadur Thapa, Shyam Sundar Bhandari and Tek Bahadur Rayamajhi for their constant support during the forest inventory. Meena Kunwar and Poorneshwor Subedi provided the satellite images. We also thank Chaudhary, Dr. Sushim Ranjan Baral and Puran Prasad Kurmi for their help with species identification in the field and at the Herbarium. Thanks also go to two anonymous reviewers for their constructive comments. This work was financially supported by Sida. The Royal Swedish Academy of Agriculture and Forestry is also acknowledged for funding the first author to present part of the results of this paper in a conference held in Washington.

References

- Anonymous. 1994. Operational Forest Management Plan for Nawalparansi District (1995–2000). Forest Research and Survey Centre, Kathmandu.
- Brown ND, Whitmore TC. 1992. Do Dipterocarp Seedlings Really Partition Tropical Rain Forest Gaps? *Royal Society of London Biological Science*, **335**: 369–378.
- Cannon CH, Peart DR, Leighton M, Kartawinata K. 1994. The structure of lowland rainforest after selective logging in West Kalimantan, Indonesia. *Forest Ecology and Management*, **67**: 49–68.
- Collins SL, Glenn SM, Gibson DJ. 1995. Experimental Analysis of Intermediate Disturbance and Initial Floristic Composition: Decoupling Cause and Effect. *Ecology*, **76**: 486–492.
- Connell JH. 1978. Diversity in tropical rain forests and coral reefs. High diversity of trees and corals is maintained only in a nonequilibrium state. *Science*, **199**: 1302–1310.
- Fulbright TE. 2004. Disturbance effects on species richness of herbaceous plants in a semi-arid habitat. *Journal of Arid Environment*, **58**: 119–133.
- Gautam KH, Devoe NN. 2006. Ecological and anthropogenic niches of sal (*Shorea robusta* Gaertn. f.) forest and prospects for multiple-product forest management - a review. *Forestry*, **79**: 81–101.
- Hubbell SP. 2001. The unified neutral theory of biodiversity and biogeography. Monographs in population biology 32. Princeton, New Jersey: Princeton University Press.
- Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, de Lao SL. 1999. Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. *Science*, **283**: 554–557.
- Jackson JK. 1994. Manual of afforestation in Nepal, second edition: Forest Research and Survey Center, Kathmandu, Nepal.
- Kennard DK, Gould K, Putz FE, Fredericksen TS, Morales F. 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. *Forest Ecology and Management*, **162**: 197–208.
- Lamb D, Erskine PD, Parrotta JA. 2005. Restoration of Degraded Tropical Forest Landscapes. *Science*, **310**: 1628–1632.
- Lindenmayer DB, Franklin JF. 2002. Conserving forest biodiversity, a comprehensive multiscaled approach. Island Press, Washington DC, USA.
- Nagaike T, Kamitani T, Nakashizuka T. 1999. The effect of shelterwood logging on the diversity of plant species in a beech (*Fagus crenata*) forest in Japan. *Forest Ecology and Management*, **118**: 161–171.
- Onaindia M, Dominguez I, Albizu I, Garbisu C, Amezcaga I. 2004. Vegetation diversity and vertical structure as indicators of forest disturbance. *Forest Ecology and Management*, **195**: 341–354.
- Pande PK. 1999. Comparative vegetation analysis and sal (*Shorea robusta*) regeneration in relation to their disturbance magnitude in some sal forests. *Tropical Ecology*, **40**: 51–61.
- Pandey SK, Shukla RP. 2001. Regeneration strategy and plant diversity status in degraded sal forests. *Current Science*, **81**: 95–102.
- Ramirez-Marcial N, Gonzalez-Espinosa M, Williams-Linera G. 2001. Anthropogenic disturbance and tree diversity in Montane Rain Forests in Chiapas, Mexico. *Forest Ecology and Management*, **154**: 311–326.
- Sagar R, Raghubanshi AS, Singh JS. 2003. Tree species composition, dispersion and diversity along a disturbance gradient in a dry tropical forest region of India. *Forest Ecology and Management*, **186**: 61–71.
- Sagar R, Singh JS. 2006. Tree density, basal area and species diversity in a disturbed dry tropical forest of northern India: implications for conservation. *Environmental Conservation*, **33**: 256–262.
- Sapkota IP, Tigabu M, Oden PC. 2009a. Species diversity and regeneration of old-growth seasonally dry *Shorea robusta* forests following gap formation. *Journal of Forestry Research*, **20**: 7–14.
- Sapkota IP, Tigabu M, Oden PC. 2009b. Spatial distribution, advanced regeneration and stand structure of Nepalese Sal (*Shorea robusta*) forests subject to disturbances of different intensities. *Forest Ecology and Management*, **257**: 1966–1975.
- Sheil D. 1999. Tropical forest diversity, environmental change and species augmentation: After the intermediate disturbance hypothesis. *Journal of Vegetation Science*, **10**: 851–860.
- Sheil D, Burslem DFRP. 2003. Disturbing hypotheses in tropical forests. *Trends in Ecology and Evolution*, **18**: 18–26.
- Swamy PS, Sundarapandian SM, Chandrasekar P, Chandrasekaran S. 2000. Plant species diversity and tree population structure of a humid tropical forest in Tamil Nadu, India. *Biodiversity and Conservation*, **9**: 1643–1669.
- Tárrega R, Calvo L, Marcos E, Taboada A. 2006. Forest structure and understorey diversity in *Quercus pyrenaica* communities with different human uses and disturbances. *Forest Ecology and Management*, **227**: 50–58.
- Timilsina N, Ross MS, Heinen JT. 2007. A community analysis of sal (*Shorea robusta*) forests in the western Terai of Nepal. *Forest Ecology and Management*, **241**: 223–234.
- van Gernerden BS, Olff H, Parren MPE, Bongers F. 2003. The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *Journal of Biogeography*, **30**: 1381–1390.
- Vetaas OR. 1997. The effect of canopy disturbance on species richness in a central Himalayan oak forest. *Plant Ecology*, **132**: 29–38.
- Webb EL, Sah RN. 2003. Structure and diversity of natural and managed sal (*Shorea robusta* Gaertn.f.) forest in the Terai of Nepal. *Forest Ecology and Management*, **176**: 337–353.
- Whittaker RH. 1970. Communities and Ecosystems. Macmillan, New York.
- Zhu JJ, Mao ZH, Hu L, Zhang JX. 2007. Plant diversity of secondary forests in response to anthropogenic disturbance levels in montane regions of northeastern China. *Journal of Forest Research*, **12**: 403–416.